tabolism of an unknown subject. An analysis of the data of actual experimentation on subjects at changing levels of nutrition shows that the changes in metabolism are not proportional to those in body surface. Surface area may not be looked upon as a determining factor in basal metabolism.

The closest prediction of the daily heat production of a subject can be made by the use of the multiple regression equations,

For men, $h = 66.4730 + 13.7516\ w + 5.0033\ s - 6.7550\ a$

For women, $h = 655.0955 + 9.5634\ w + 1.8496\ s - 4.6756\ a$

where h = total heat production per 24 hours, w = weight in kilograms, s = stature in centimeters, and a = age in years. These equations have been tabulated for values of weight from 25.0 to 124.9 kgm., for stature from 151 to 200 cm., and for age from 21 to 70 years, so that the most probable basal metabolism of an unknown subject may be easily determined.

Such tables should render service in clinical and other fields of applied calorimetry. Their usefulness has been demonstrated in testing the typical or atypical nature of series of metabolism measurements, in investigating the differentiation of the sexes with respect to metabolic activity, of the metabolism of athletes as compared with non-athletic individuals, and of individuals suffering from disease.

The detailed measurements and statistical constants, with full discussions of pertinent literature, are about to appear in Publication No. 279 of the Carnegie Institution of Washington.

SEX AND SEX INTERGRADES IN CLADOCERA

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There is probably no one factor in the biological world of greater interest and importance than sex.

Most plants are dioecious, producing the reproductive cells of both sexes within the same individual organism. Several lower animals are normally hermaphroditic but by far the larger part of the forms in the animal world are unisexual.

So general is unisexuality in animals and so little thought do we in general give to the comparatively few normally hermaphroditic forms that we are accustomed to think of maleness and femaleness as opposed and mutually exclusive states which cannot coexist in the same organism. We are accustomed to think of maleness as indicating the possession not only of a sperm-producing gland and accessory reproductive structures but also the possession of the peculiar secondary sex character—structural, physiological, and even psychological and behavior characteristics. The term female implies pro-

nounced characteristics contrasting with those of a male on these several points. In other words maleness and femaleness are generally assumed to indicate definite and precise alternative and opposing states only one of which may obtain in the same individual organism.

With unisexual forms known deviations from the supposed mutually exclusive conditions of maleness and femaleness were until recently confined to a comparatively few cases of hermaphroditism and gynandromorphism. Such cases have been defined as sex mosaics—definite gonads or portions of the gonads or other parts of the body being described as distinctly of one or of the other sex.

However, there are at least three known cases of the common occurrence of unmistakable intermediate sex forms—sex intergrades. These are Riddle's hybrid pigeons,[1] Goldschmidt's hybrid gypsy moths[2] and the writer's Cladocera material. These are not sex mosaics but sex intergrades.[3] That is to say, they are not fully male in certain definite portions of the body and fully female in other portions but frequently as a whole and (in the writer's material) almost always in certain parts they clearly possess both femaleness and maleness—they are as a whole and by parts distinctly intermediate as regards sex.

In the Cladocera material there sometimes occurs an individual which might very readily be considered a sex mosaic, inasmuch as its complement of secondary sex characters consists of some apparently fully male and some fully female characters. But the majority of these secondary sex characters are obviously intermediate between the fully female and the fully male character, and there are comparatively few of the sex intergrades which do not have one or more such intermediate sex characters. These intergrading sex characters clearly indicate that we have to do not with sex-mosaics but with sex intergrades.

In Cladocera the population ordinarily consists entirely of females and reproduction is by means of parthenogenetically developing eggs. Occasionally males appear and some females produce the less usual type of egg which must be fertilized in order to develop. This occasional sexual reproduction has given rise to the notion that there is an innate sexual cycle in these forms.

In all the many lines of the writer's stock however, previous to the appearance of the sex intergrade strains, males were seen only two or three times and in as many lines.[4] Though no sexual reproduction has occurred in any case the various lines continue to reproduce with their original vigor. Hence as applied to this material the supposed innate sexual cycle seems quite an unwarranted assumption.

In the writer's stock previous to the appearance of the recognized sex intergrade strains there were a few individuals of one strain of Daphnia longispina which may have been sex intergrades. These individuals failed to reproduce but it is probable that they were really sex intergrades and that

there would have been intergrades among their offspring if they had reproduced at all.

Undoubted sex intergrades were first found and propagated in the writer's stock in one of the strains of Simocephalus vetulus. None have been seen in any strain of this species except in direct descendants of the initially discovered sex intergrade mother. Great numbers of Simocephalus vetulus have been examined microscopically especially in the last sixteen months and while normal males have been found on occasion, no sex intergrades have been discovered. This is true in spite of the fact that the sex characters are the characters especially scrutinized and that in the aggregate many thousands of Simocephalus vetulus have been examined. Hence in Simocephalus vetulus the occurrence of clearly marked sex intergrades is by no means to be considered a frequent phenomenon.

In Daphnia longispina, however, sex intergrades have been discovered in all three of the strains of line 768, and we now have in the laboratory well established strains of sex intergrades from two of these three strains. Sex intergrades have been found also in two of the three other laboratory lines of this species. Coupled with the fact that the observation of probable sex intergrades at an earlier time was also in this species, the occurrence of sex intergrades in all except one of the six strains of Daphnia longispina in the laboratory, seems to indicate that for this species the production of sex intergrade strains is not such an unusual phenomenon. However, one significant fact should not be overlooked, namely, that except for close scrutiny of the cultures including microscopic examination of great numbers of individuals the occurrence of intergrades would not have been suspected.

Though in recent months males have been found in all except one strain of all the stock of the seven species of Cladocera reared in the laboratory no intergrades have been discovered in either Daphnia pulex, Simocephalus serrulatus, or in three species of Moina, or in Simocephalus vetulus except in descendants of the original sex intergrade mothers. The sexual characters of thousands of individuals of each of these species have been microscopically examined.

Within the stock in the laboratory it then seems fairly clear that the occurrence of sex intergrades is quite unusual, though intergrades have been found in most of the strains of Daphnia longispina.

The sex intergrade strain of Simocephalus vetulus originated in October, 1915, in line 740 in its 131st laboratory generation during a period of conditions of poor nutrition in the stock due to unsatisfactory food.

The secondary sex characters and other matters relating to this intergrade strain have been discussed in some detail in another paper[5] (Banta, 1916) and need not be considered further here.

The sex array is extensive. There occurs almost every combination of male and female primary and secondary sex characters. This coupled with the fact that most of the secondary sex characters occur very frequently in an

intermediate condition serves to make the sex array in Simocephalus very extensive indeed. In fact a precise classification is quite impossible and only an extremely relative classification is at all feasible.

Since the origin of sex intergrades in line 740, the sex intergrade strains have descended for nearly three years (about 57 generations). The character of the stock seems unchanged—the sex array and proportions of the various apparently pure sex forms and intergrades of different sorts continues as it was when the intergrade stock first appeared.

The sex intergrades in Daphnia longispina were first observed in May, 1917. They appeared in one of the three strains of line 768. This strain was not passing through a period of unfavorable conditions at that time nor was there anything unusual observed in its behavior except the occurrence of sex intergrades. It is indeed not certain that intergrades may not have occurred sparingly for a few generations before they were discovered. The first intergrade mothers noted in this strain produced many sex intergrades among their offspring. Several intergrade strains were at once isolated from this stock and placed under observation.

The secondary sex characters in Daphnia longispina are as follows: (1) *Body size*—the females are larger than the males; (2) *Character of the head outline*—the ventral margin of the head in the female slopes almost uniformly to the tip of a pointed rostrum or beak while in the male the beak is absent; (3) and (4) *Characters of the first (rudimentary) antennae*—the paired female first antennae are represented only by slight eminences from which arise a few sensory stylets, while in the male the first antennae are movable structures three-fifths as long as the head. At its distal end each male antenna is armed with a stout bristle in addition to the sensory stylets possessed by the female; (5) and (6) *Character of the breast margins*—the female ventral carapace margins are almost uniformly rounded from the anterior portion backward. In the male these margins are angulated almost to 90 degrees in the region nearest the head. Further in the region of this angle these margins are fringed with hairs in the male while none occur in the female; (7) and (8) *Character of the first legs*—in the female the terminal joint of each of the first pair of legs is not armed with a hook, while this segment in the male bears a stout hook.

That these characters are distinctive of the two sexes is shown by the fact that they occur practically without deviation in wild stock, and in females[6] and males of the stock not producing intergrades, as well as in the extremes of the series in the sex intergrade strains.

The array of sex intergrades in Daphnia longispina is less extensive than in the sex intergrade strains of Simocephalus vetulus in that male sex intergrades (i.e., intergrades with testes) are almost or quite lacking and further that males are extremely scarce in the sex intergrade strains of this species. That is to say that toward the male end of the series where should occur numbers of male intergrades and ostensibly normal males—if the sex array

were complete and uniform—the numbers of male intergrades and apparently fully male individuals are few and the series is not at all diverse. On the other hand with the Simocephalus vetulus sex intergrade stock normal males are abundant and male intergrades are common in occurrence. In other words the sex intergrade strains of Daphnia longispina are more female and correspondingly less male than those of Simocephalus vetulus.

In another manner the sex intergrades of Daphnia longispina differ from those of Simocephalus vetulus. Each of the several secondary sex characters in Daphnia longispina is subject to intermediate development and occurs in all intergrading stages from the fully female to the fully male secondary character; whereas some of the secondary sex characters in Simocephalus vetulus are not such as to readily show so wide a range of intermediate conditions.

One rarely finds a Daphnia longispina intergrade which has its full complement of secondary sex characters—each character apparently fully male or fully female. The vast majority of the Daphnia longispina intergrades have at least three (of a total of eight) secondary sex characters distinctly intermediate between the male and female in point of sex significance, while frequently all of the secondary sex characters partake of the intermediate condition.

With the sex intergrade strains of both Simocephalus vetulus and Daphnia longispina the character of offspring is somewhat correlated with the secondary sex characters of the mother. The more maleness the female intergrade possesses the more highly male in general will be the character of the offspring. In most cases the relative amount of maleness and femaleness possessed by the different individuals of a brood of young is extremely variable; but ordinarily if the mother is highly intergrade in several characters the young, while quite variable will also on the average be relatively highly male in their characteristics. On the other hand a female from a sex intergrade strain who herself shows little or no evidence of maleness will ordinarily produce young with few or slight male characters, though the young are on the average usually more male than the slightly intergrade mother herself.

An extremely intergrade mother, whose secondary sex characters are all largely or fully male, is in most cases sterile or nearly so. This is notably true of the Simocephalus vetulus sex intergrades in which a female intergrade with a full complement of male secondary sex characters has not been known to reproduce. On the other hand a female intergrade with few male or only slightly male secondary sex characters is usually highly productive of young.

Sex intergrade production would seem to be the result of a disturbed balance, a condition which—obviously in many individuals and probably in all individuals, *at least* of the sex intergrade strains—is a struggle of two nearly equal factors or sets of factors, the one making for maleness, the other for femaleness. The result of this struggle of factors is individuals ostensibly male in part and female in part and obviously intermediate in part—but as a whole distinctly intermediate in sex characters.

The point of perhaps greatest importance lies in the findings of sex intergrades in a number of lines of a second species of Cladocera—in fact in five out of six lines of that species which have been reared in the laboratory. In addition De la Vaulx records[7] what are almost certainly such intergrade individuals in Daphnia atkinsoni. These extensions of the known occurrences of sex intergrades among Cladocera indicate that a condition of sex intergradedness in Cladocera is less unusual than the writer formerly supposed—that maleness and femaleness are even less exclusive phenomena so far as indicated by morphological characters in Cladocera than was believed. In this material the disturbances of the balance of the factors or sets of factors making for sex is less unusual than would seem probable if maleness and femaleness were really generally mutually exclusive.

From such clear cases of sex intermediates one wonders if maleness and femaleness are really mutually exclusive in those Cladocera individuals which morphologically show no unlike sex characters. It seems extremely probable that they are not, particularly in view of the fact that in sex intergrade strains apparently normal females frequently produce young of widely divergent types of sex intergrades. Even in the 'normal' strains one is certainly justified in thinking that maleness and femaleness are not complete and mutually exclusive states but that in these apparently normal sex forms, too, sex is also relative—differing from the so-called sex intergrades not in kind but merely in degree, not qualitatively but quantitatively.

With the relativity of sex so emphatically shown in hybrid pigeons, in hybrid moths and in different species of Cladocera one wonders if the relativity of sex ends with pigeons, gypsy moths and water fleas. There seems every reason to think it does not. We are coming to the time when it would seem imperative to revise our notions of the fixity of sex. The clear cases of sex intergrades or sex intermediates just referred to seem no more nor no less illustrations of the relativity of sex than one sees in the 'crowing hen' and the 'sitting cock' or in the masculine woman and in the man who in almost intangible physical characteristics, in speech, in dress, in tastes and habits of behavior, and in methods of thought reveals himself as lacking in something which makes for the fully equipped male and as possessing qualities ordinarily recognized as characteristics of the female.

Further it does not seem necessary to suppose that relativity of sex is restricted to cases in which its very conspicuousness forces itself upon our unwilling attention in opposition to our fixed conceptions of maleness and femaleness as complete, opposed, and mutually exclusive phenomena. Indeed the more reasonable supposition is that sex is always relative, that while most sexual individuals of whatever species are prevailingly male or prevailingly female every individual may have something of the other sex intermingled with its prevailing sexual characters.

[1] Riddle, Oscar, *Carnegie Inst. Washington Year Book*, **12**, 1913, (322); also *Amer. Nat.* **50**, 1916, (385–410).

[2] Goldschmidt, R., *Zs. ind. Abs.-Vererbungslehre*, **7**, 1912, (1–62); also these PROCEEDINGS **2**, 1916, (53–58).

[3] Called sex intermediates by Riddle; intersexual forms by Goldschmidt.

[4] There is one reference in the literature to androgynous Cladocera (in Daphnia atkinsoni). Judging from De la Vaulx's description these individuals, which he called gynandromorphs, were almost certainly sex intergrades.

[5] Banta, A. M., these PROCEEDINGS, **2**, 1916, (578–583).

[6] The writer used the terms female and male with the mental reservation that inasmuch as femaleness and maleness are now definitely known to be relative in some cases they may be relative in *all individuals* and that the terms female and male are themselves to be considered relative not only in Cladocera, pigeons and moths but perhaps also in all animal and plant forms in which sex is known to occur.

[7] Vaulx, R. de la, *Bull. Soc. Zool. France*, **40**, 1916, (102–104, 194–197,

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ON THE METHOD OF PROGRESSION IN POLYCLADS[1]

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Turbellarians are able to make progress through the water by means of muscular movements of the body as a whole, or of its lateral extensions; their creeping progression on a solid substratum, however, has usually been attributed to the action of cilia. According to Stringer (1917),[2] the locomotion of planarians is effected by muscular contractions, which may be organized after the manner of the locomotor wave upon the foot of a monotaxic gastropod (cf. Parker, 1911),[3] the ciliary activity taking no necessary part in the locomotion. Some observations, which may here be briefly noted, tend to confirm the nature of this finding, and add to the variety of known muscular creeping movements in turbellarians.

One species of Leptoplana, occurring at Bermuda in moderate numbers, differs from the more frequently encountered L. lactoalba Verr., approaching more nearly the form L. lactoalba var. tincta Verr. It is found on the under surfaces of stones, near high water level, and is commonly about 3.5 cms. long. If, out of water, a stone bearing one of these leptoplanas is turned over, exposing the animal to light, it creeps about upon the moist surface. The worm also creeps rapidly under water, and in addition is a vigorous swimmer. It has usually been believed that in Leptoplana "creeping is a uniform gliding movement, caused by the cilia of the ventral surface, aided perhaps [how?] by the longitudinal muscle layer of this surface" (Gamble, 1901, p. 10).[4] While this may very well seem to be the case in L. tremellaris (Gamble, loc. cit.), and in several other species which I have observed, it is distinctly not true of the form which I may refer to as L. 'tincta.' The ventral surface of this platode is richly ciliated, and in creeping it deposits an appreciable slime-track, such as that in which the cilia of triclads have